Comparative morphology of the alimentary tract and its glandular derivatives of captive bustards

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ABSTRACT

This study describes the gross anatomy of the alimentary tract of Houbara Bustards (*Chlamydotis undulata macqueenii*), Kori Bustards (*Ardeotis kori*), Rufous-crested Bustards (*Eupodotis ruficrista*) and White-bellied Bustards (*Eupodotis senegalensis*) maintained in captivity by the National Avian Research Center in the United Arab Emirates. The morphology of the alimentary tract and the proportions of each region were similar in all 4 species. The length of the oesophagus, combined proventriculus and ventriculus, small intestine, and large intestine formed 24.2–28.4%, 7.3–9.7%, 40.5–55.1% and 9.1–14.7% of the total alimentary tract length respectively. Neither crop nor oesophageal enlargement was observed in the birds examined in this study, although male Kori Bustards possessed a saccus oralis in the oropharyngeal cavity. Oesophagi, proventriculi, ventriculi, caeca and large intestine were well developed in all species. The small intestine was shorter than that of other avian herbivores and granivores when compared on a bodyweight basis. The well differentiated stomachs and well developed caeca of the bustards examined in this study are characteristic of omnivores. Analysis of the mean lengths of the alimentary tract components and weight of the liver and pancreas showed sexual dimorphism in cases where male and female data were available for direct comparison.

Key words: Avian anatomy; gastrointestinal tract; Otididae; Chlamydotis; Ardeotis; Eupodotis.

INTRODUCTION

Bustards belong to the Otididae family and are medium sized to very large terrestrial birds mainly inhabiting open plains and semidesert regions of the world. Free-living bustard populations have been declining throughout the world since the second world war due to excessive hunting, overgrazing of habitat, and agricultural and industrial development (Johnsgard, 1991). Over the last 10–15 years there has been a surge of interest in the conservation of bustards, in particular the Houbara Bustard (*Chlamydotis undulata macqueenii*), and large captive breeding and restoration programmes for this species have been established in the Middle East.

A large body of knowledge exists on the anatomy of the alimentary tract of many other birds (Ziswiler & Farner, 1972; McLelland, 1975, 1979*a*; Nickel et al. 1977; King & McLelland, 1984) but, very little has been published about the alimentary tract of bustard species. Beddard (1898, 1910), commented briefly on the mesenteric relations of the alimentary tract of the Houbara Bustard and the Australian Bustard (*Ardeotis australis*). Mitchell (1895, 1901), included a brief account of the alimentary tract of the Great Bustard (*Otis tarda*) in his description of the anatomy of the Gruiformes. Most recently, Maloiy et al. (1987) published a comparative paper on the gross anatomy of the alimentary tract of the Kori Bustard (*Ardeotis kori*) and the Secretary Bird (*Sagittarius serpentarius*).

Management of bustards in captivity is handicapped by the paucity of biomedical data. As a consequence comprehensive research programmes, including anatomical and pharmacological studies, have been instigated by the National Avian Research Center (NARC). An understanding of the anatomy of

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the alimentary tract of bustards was considered important, because it is known that anatomical differences can cause significant variation in drug absorption from the oral route in animals (Dorrestein & Van Miert, 1988; Kararli, 1989). Such studies would also prove useful in relation to medical, surgical, propagation and nutritional management of these birds in captivity. To the knowledge of the authors, no published reports exist describing the normal anatomy of the alimentary tract of other bustard species. The present study was undertaken to investigate the anatomy of the alimentary tract and its glandular derivatives of 4 bustard species maintained in captivity by the NARC.

MATERIALS AND METHODS

Four species of adult captive bustards of mixed sex (38) were examined from April 1994 to October 1996. The numbers and sex of each species examined included 21 Houbara Bustards (8 male and 13 female), 10 Kori Bustards (5 male and 5 female), 5 female Rufous-crested Bustards (*Eupodotis ruficrista*) and 2 White-bellied Bustards (*Eupodotis senegalensis*) of either sex. All birds, except 4 Rufous-crested Bustards, which were captive-bred and reared at NARC, were derived from the wild 6–10 y previously. Birds were maintained in naturalistic aviaries and fed on a diet of fresh apple, cabbage, mince and a manufactured pellet, supplemented with laboratory mice and meal-worms.

Postmortem examinations were performed within 24 h of death on fresh or refrigerated carcasses. Birds that were euthanased had been hospitalised for between 1 and 7 d before death. Carcasses were weighed to the nearest gram at postmortem.

Alimentary tract measurements

The alimentary tract was carefully dissected and the entire length from the proximal oesophagus to the cloaca was placed on a tray. The tract was stripped of fat deposits and the mesentery and each component was separated, placed unstretched in a straight line and its total length measured. The components of the alimentary tract measured are presented in Figure 11. Length measurements were taken of the oesophagus, proventriculus, ventriculus, small intestine (duodenum, jejunum, and ileum), caeca, and combined rectum and cloaca. The combined rectum and cloaca were measured from the ileocaecal opening to the lip of the vent. The ventriculus was measured when full from the isthmus gastris to the caudal extremity of the saccus caudalis. Additionally, the height and width of the full ventriculus were measured. The height was derived from the distance between the crassus caudodorsalis and crassus cranioventralis muscles and the width was the distance between the centrum tendineum on either side of the ventriculus. The length of the dorsal lobe of the pancreas was also measured. The empty ventriculus (emptied of contents, washed and dried with a paper towel), the dorsal and ventral lobes of the pancreas and liver were weighed to the nearest 0.01 g.

The length of the entire alimentary tract was defined as the sum of oesophagus, proventriculus, ventriculus, small intestine, combined rectum and cloaca. This value was used to calculate the percentage contribution of each component to the entire tract. Alimentary tract measurements for males and females were described separately and the data were analysed by Student's t test (2-tailed test assuming equal variance) using Microsoft Excel (Microsoft Corporation, USA) to assess sex differences. A written record of observations on the gross appearance of the alimentary tract was kept at each dissection. Photographs were taken of one dissection of a Houbara Bustard and a Kori Bustard. Line drawings of the oral cavity, the ventriculus and the entire alimentary tract of the Houbara Bustard were produced from these photographs. A description of the gross appearance of the alimentary tract was prepared from the written records and the photographs. Anatomical terms used are as defined by McLelland (1979*b*) in the Nomina Anatomica Avium. For comparative purposes, alimentary tract measurements were collected from 10 normal adult female, Bantam Chickens (*Gallus domesticus*) that were euthanased during this study. These birds were maintained on commercially available layer pellets.

RESULTS

Postmortem examination

The causes of death of the bustards in this group included trauma (17), euthanasia for untreatable fractures, dislocations or chronic lameness (8), capture paresis (3), post-handling death (1), anaesthesia-related deaths (3) and unexplained death with trauma suspected (6). No gross pathological abnormalities were observed in the alimentary tracts of these birds on examination.

Alimentary tract measurements

Comparative measurements of the mean length of each component of the alimentary tract for each

Table 1. *Alimentary tract measurements of 4 species of captive bustards**

Species	RCB	WBB	WBB	HB	HB	KB	KB
Number	5	1	1	13	8	5	5
Sex	F	F	M	F	M		M
Carcass weight (g)	509.4 ± 17.81 (5)	916	973	1016.1 ± 24.95 (13)	1270.9 ± 32.84 (8)	4323.2 ± 470.9 (5)	10 226 ± 1418 (5)
Oesophagus (l/mm)	169 ± 16 (2)	190	240	232 ± 9.97 (6)	287.6 ± 7.82 (8)	402.5 ± 2.5 (2)	600 (1)
Proventriculus (l/mm)	22.86 ± 1.56 (3)	25.7	26	26.9 ± 1.79 (9)	30 ± 1.27 (8)	48.3 (1)	56 ± 0 (2)
Ventriculus (l/mm)	44.43 ± 4.23 (4)	35.5	50	44 ± 1.01 (12)	51.5 ± 2.49 (8)	83.3 ± 4.98 (3)	104 ± 7 (3)
Ventriculus (w/mm)	34.4 ± 3.35 (3)	23.5	35	29.29 ± 0.66 (10)	30.38 ± 1.01 (8)	44 ± 3.61 (3)	57.3 ± 5.48 (3)
Ventriculus (h/mm)	22.4 (1)	nd	19	20.28 ± 1.75 (4)	22.6 ± 0.9 (2)	29 (1)	33 (1)
Ventriculus (wt/g)	11.25 ± 1.18 (3)	8.88	12.78	12.39 ± 0.59 (10)	17.32 ± 1.72 (8)	53 ± 11 (2)	114.5 ± 5.5 (2)
Pancreas (l/mm)	25.9 (1)	nd	26	36.35 ± 2.3 (9)	41.3 ± 4.2 (4)	82.1 (1)	85 ± 10 (2)
Pancreas (wt/g)	0.48 ± 0.08 (2)	nd	0.72	0.86 ± 0.07 (8)	0.98 ± 0.12 (3)	nd	nd
Liver (wt/g)	9.43 ± 0.87 (5)	14.1	20.44	19.54 ± 0.41 (12)	25.49 ± 2.15 (7)	72 ± 13.88 (4)	143.8 ± 9.52 (5)
Small intestine (l/mm)	380.4 ± 37.65 (5)	350	470	403.4 ± 11.6 (12)	451.25 ± 19.27 (8)	791 ± 74.52 (5)	1151 ± 51.1 (5)
Caecum (l/mm)	109.28 ± 7.37 (5)	84.5	205	113.9 ± 6.22 (13)	154.3 ± 14.66 (8)	226.4 ± 15.97 (5)	334 ± 15.76 (5)
Rectum and cloaca (l/mm)	75.2 ± 9.37 (5)	105	160	108.9 ± 7.65 (12)	130.29 ± 9.18 (8)	150 ± 16.83 (4)	259 ± 22.27 (5)

* Means ± S.E.M. (n); nd, no data; l, length; w, width; h, height; wt, weight; RCB, Rufous-crested Bustard; WBB, White-bellied Bustard; HB, Houbara Bustard; KB, Kori Bustard.

Table 2. *Dimensions of the alimentary tract of bustards compared with Bantam Chickens in order of bodyweight*

Species	Kori bustard (m)	Kori bustard (f)	Houbara bustard (m)	Bantam chicken (f)	Houbara bustard (f)	White-bellied bustard (m)	White-bellied bustard (f)	Rufous-crested bustard (f)
Bodyweight (kg)	10.22	4.32	1.27	1.14	1.02	0.973	0.916	0.51
Oesophagus								
Length (m)	0.6	0.4	0.29	0.23	0.23	0.24	0.19	0.17
Total weight	27.6	24.2	26.1	13.9	28.4	26.1	26.8	24.6
Proventriculus + gizzard								
Length (m)	0.16	0.13	0.081	0.069	0.071	0.049	0.061	0.067
Total length (%)	7.4	7.8	7.3	4.2	8.8	5.3	8.6	9.7
SI								
Length (m)	1.15	0.79	0.45	1.24	0.4	0.47	0.35	0.38
Total length (%)	42.6	47.9	40.5	74.7	49.1	51.1	49.3	55.1
Length/BW ($m\ kg^{-1}$)	0.11	0.18	0.36	0.9	0.39	0.48	0.38	0.75
Caecum								
Length (m)	0.33	0.23	0.15	0.16	0.11	0.21	0.085	0.11
Length/BW ($m\ kg^{-1}$)	0.032	0.053	0.12	0.14	0.11	0.22	0.093	0.22
Rectum + cloaca								
Length (m)	0.26	0.15	0.13	0.12	0.11	0.16	0.11	0.075
Total length (%)	11.98	9.1	11.7	7.2	13.6	17.4	15.5	14.7
Length/BW ($m\ kg^{-1}$)	0.025	0.034	0.1	0.11	0.11	0.16	0.12	0.15
Total gut								
Length (m)	2.17	1.65	1.11	1.66	0.81	0.92	0.71	0.69
Length B/W ($m\ kg^{-1}$)	0.21	0.38	0.88	1.46	0.79	0.95	0.78	1.35

species are presented in Table 1. The dimensions of alimentary tract measurements of Houbara, Kori, and Rufous-crested Bustards in the current study are compared with Bantam Chickens (Table 2). The proportions of each region were similar in all species of bustards examined in the study. The data for the white-bellied bustards showed some discrepancies, but this probably reflects the fact that only 1 individual of each sex was examined. Excluding the White-bellied Bustard data, the length of the oesophagi,

Table 3. *Percentage of total bodyweight of the empty ventriculus, pancreas and liver of captive bustards and bantam chickens from the current study*

Species (sex)	RCB (f)	WBB (f)	WBB (m)	HB (f)	HB (m)	KB (f)	KB (m)	Bantam (f)
Ventriculus (%)	2.21	0.97	1.31	1.22	1.36	1.23	1.12	1.99
Pancreas (%)	0.094	nd	0.074	0.084	0.076	nd	nd	0.23
Liver (%)	1.85	1.53	2.1	1.92	2.01	1.66	1.41	2.94

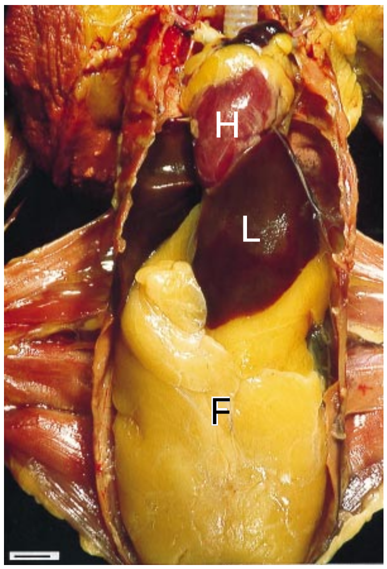

Fig. 1. Ventral view of the thorax and abdomen of a Houbara Bustard with the sternum and abdominal wall removed. The abdominal contents are covered ventrally by a double-layered fat-laden fold (F) of peritoneum, the posthepatic septum. The only organs which are not covered are the right and left lobes of the liver (L) and the heart (H). Bar, 10 mm.

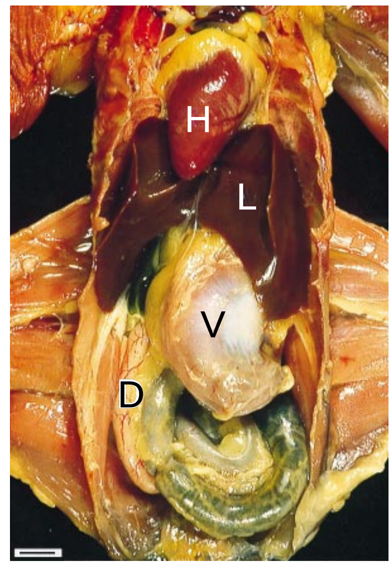

Fig. 2. Ventral view of the thoracoabdominal cavity of a Houbara Bustard. This is the same bird as shown in Figure 1 but with the posthepatic septum removed. L, liver; H, heart. On the left side of the abdomen lies the ventriculus (V) and on the right side lies the narrow U-shaped loop, the ansa duodenalis, of the duodenum (D). The caeca are visible below the ventriculus. Bar, 10 mm.

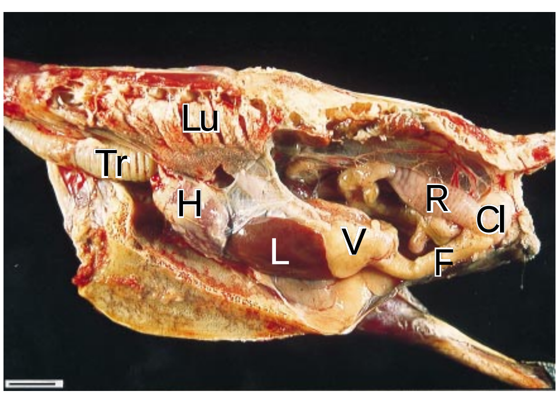

Fig. 3. Right lateral view of the thoracoabdominal cavity of a Houbara Bustard. The following viscera are visible; lung (Lu), heart (H), trachea (Tr), liver (L), ventriculus (V), kidney, caecum (C), rectum (R) and cloaca (Cl). F, double-layered fat-laden fold. Bar, 20 mm.

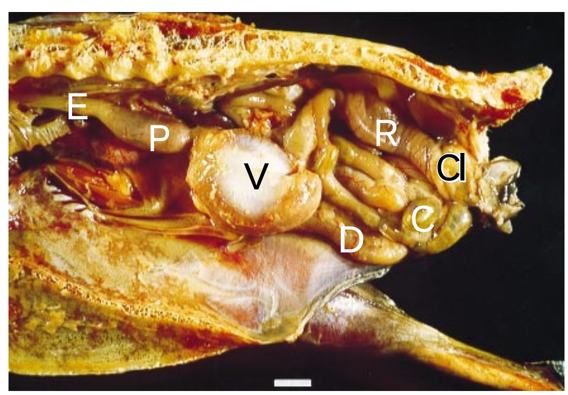

Fig. 4. Right lateral view of the thoracoabdominal cavity of a Houbara Bustard. The liver has been removed, and in addition to the viscera in Figure 3 the oesophagus (E) and the proventriculus (P) are visible. Other abbreviations as in previous figures. Bar, 12 mm.

combined proventriculi and ventriculus, small intestine, and the combined rectum plus cloaca formed 24.2–28.4 %, 7.3–9.7 %, 40.5–55.1 %, and 9.1–14.7 % of the total alimentary tract length, respectively. The percentage of the mean weight of the empty ventriculus (with cuticle), the pancreas and liver to the mean carcass weight for each bustard species and the bantam chickens are presented in Table 3.

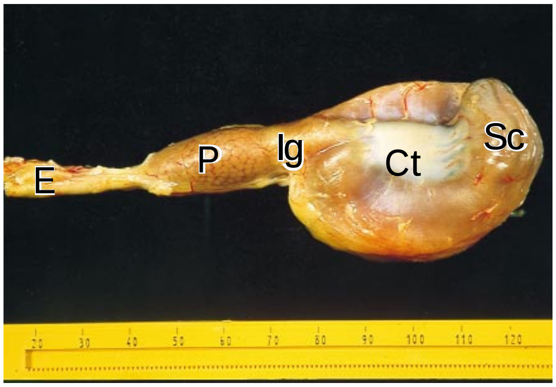

Fig. 5. Stomach of a Houbara Bustard (left lateral view). The stomach consists mainly of a cranial glandular compartment or proventriculus (P) and a caudal muscular compartment or ventriculus. The isthmus gastris (Ig), centrum tendineum (Ct) and the saccus caudalis (Sc) are marked. E, oesophagus. Scale in mm.

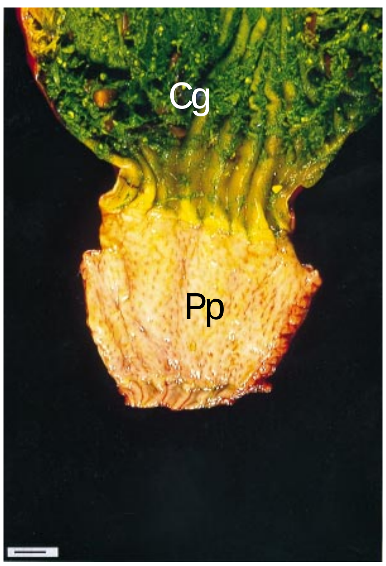

Fig. 6. Stomach of a Kori Bustard. Well developed papillae proventriculus (Pp) can be seen projecting into the lumen of the proventriculus. Lining the inner surface of the ventriculus is a hardened membrane, the cuticula gastrica (Cg). Bar, 10 mm.

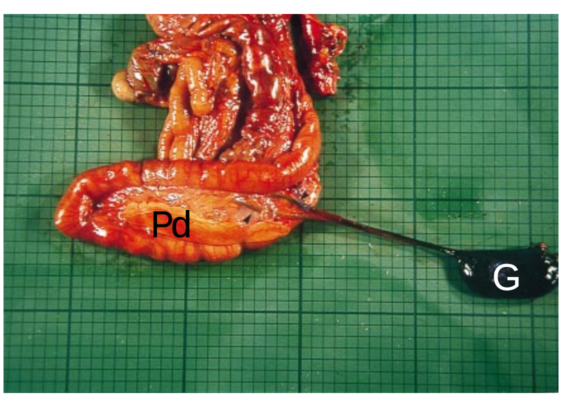

Fig. 7. Duodenal loop of a Kori Bustard illustrating the dorsal lobe of the pancreas (Pd) and the gall bladder (G) and the bile ducts (arrows). One small grid square represents 5 mm.

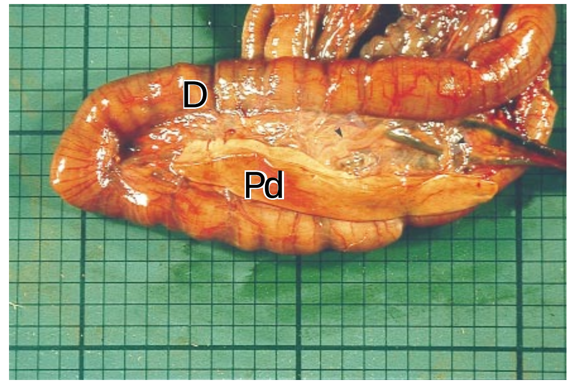

Fig. 8. Duodenal loop of a Kori Bustard illustrating the dorsal lobe of the pancreas (Pd) and the pancreatic ducts (arrows) D, duodenum. One small grid square represents 5 mm.

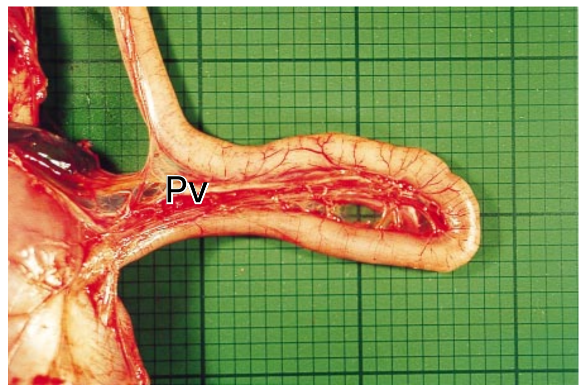

Fig. 9. Duodenal loop of a Kori Bustard illustrating the ventral lobe of the pancreas (Pv). One small grid square represents 5 mm.

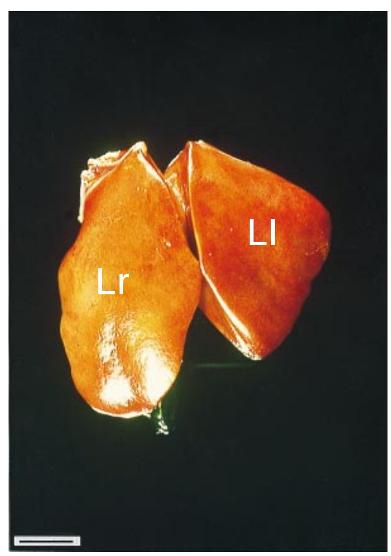

Fig. 10. Liver of a Houbara Bustard. It consists of a right (Lr) and a left lobe (Ll), the right lobe being larger than the left lobe which is not subdivided.

Alimentary tract description

The alimentary tract of all species of bustards consisted of a cavum oralis, pharynx, oesophagus, proventriculus, ventriculus, small intestine (consisting

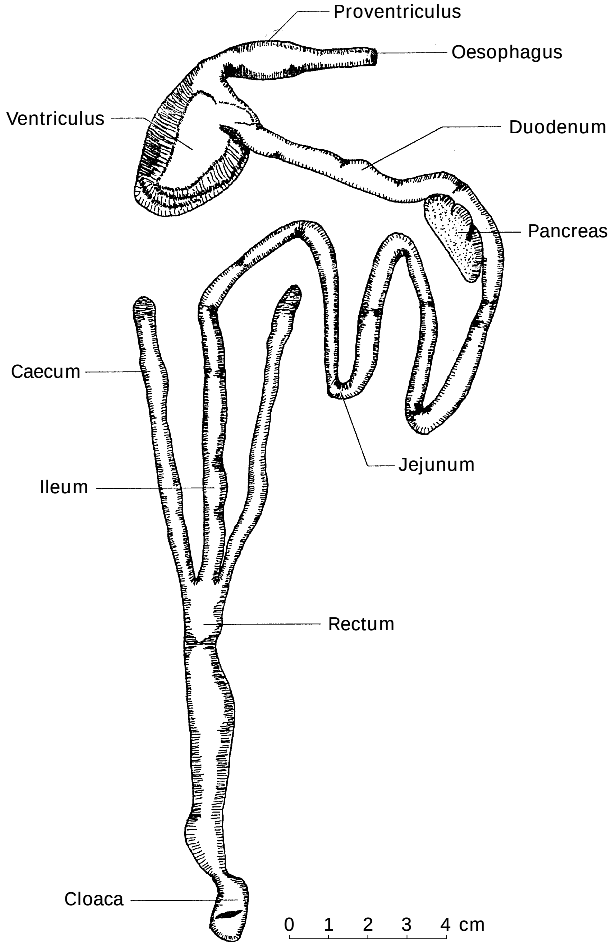

Fig. 11. Alimentary tract of an adult Houbara Bustard.

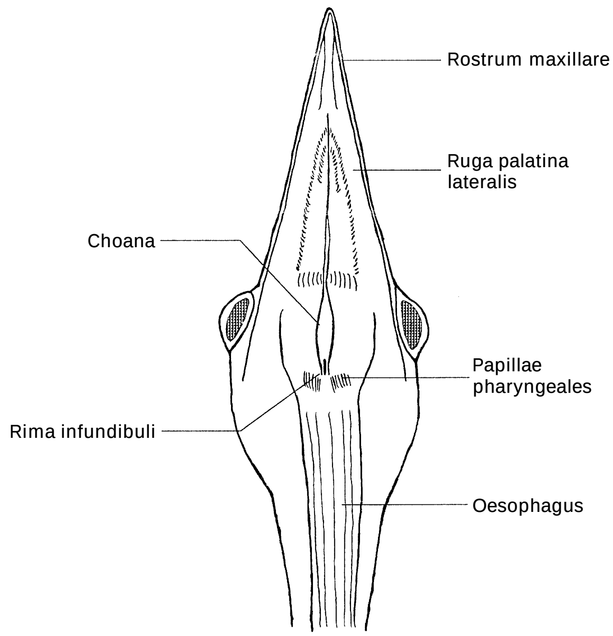

Fig. 12. Roof of the cavitas oralis and pharynx of an adult Houbara Bustard.

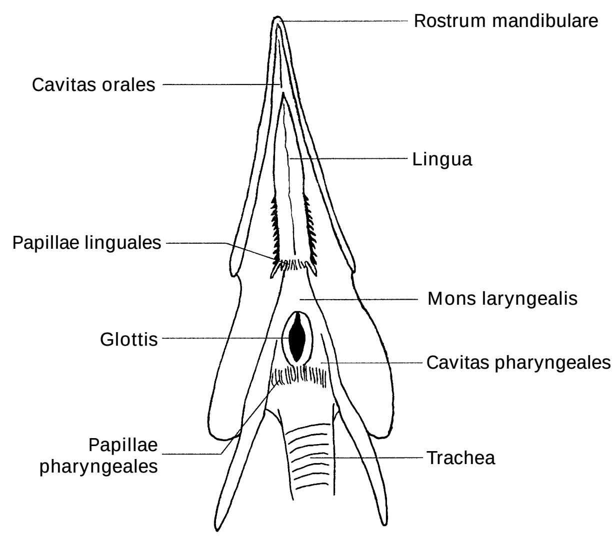

Fig. 13. Floor of the cavitas oralis and pharynx of an adult Houbara Bustard.

of duodenum, jejunum and ileum), large intestine (consisting of paired caeca and a rectum) and cloaca. The general descriptions of the morphology of the alimentary tract refer to all the species of bustards. Any differences observed between species are described separately.

Photographs of the dissection and layout of the alimentary tract within the body cavity of the Houbara Bustard are presented in Figures 1–4. Photographs of the components of the alimentary tract are given in Figures 5–10. Line drawings of the entire alimentary tract, cavum oralis, pharynx and the stomach of the adult Houbara Bustard are presented in Figures 11–14.

Cavum oralis and pharynx

In birds, the cavum oralis and pharynx form a common chamber which is referred to as the oropharynx (McLelland, 1979*b*). The roof of the oropharyngeal cavity was formed by an incomplete hard palate which extended caudally into the choana, which was a fissure that continued longitudinally in the midline of the palate (Fig. 12). The oral and nasal cavities communicated through the choana. The choana possessed a narrow rostral and an enlarged caudal portions. Its rostral portion lay close to the dorsal surface of the tongue. The palate was covered by a mucous membrane which had a number of ridges and papillae. Extending longitudinally along each side of the palate and caudally to the level of the junction of the narrow and wide parts of the choanal slit was the ruga palatina lateralis. On either side of the choana, a pair of caudally directed papillae extended

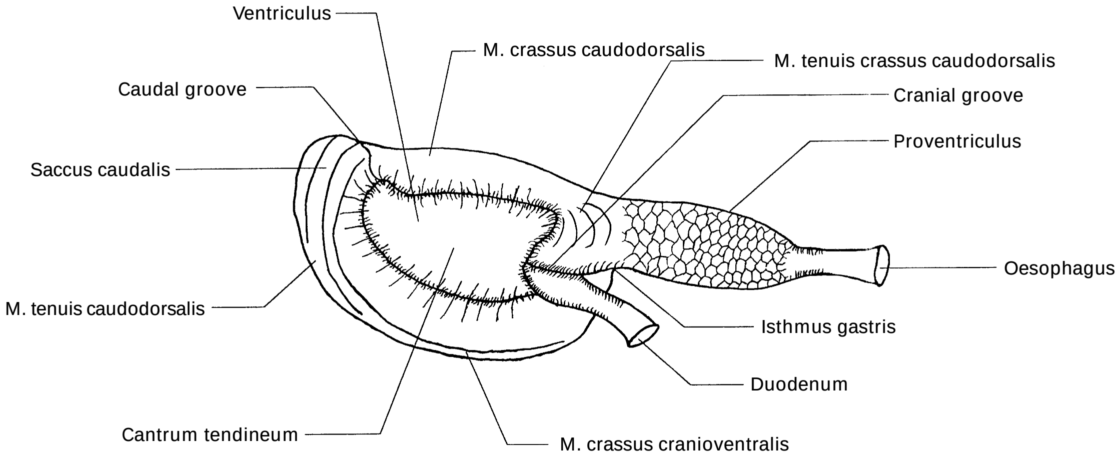

Fig. 14. Exterior of stomach of an adult Houbara Bustard. Lateral aspect, right side.

longitudinally along the roof of the palate. One row was medial to the lateral ridge on either side of the choana and extended caudally to the level of the junction of the narrow and wide parts of the choanal slit. The other row was close to the midline on either side of the choana and extended for approximately a quarter of the length of the rostral palate. A third row of transverse papillae was present on either side of the midline between the junction of the narrow and wide parts of the choanal slit. These papillae formed the papillae pharyngeales.

Lying in the floor of the oropharyngeal cavity, in a fossa between the rami of the lower mandible, was the lingua (Fig. 13). The lingua which could not be protruded was arrow shaped with serrations along its edges (from the mid to distal portion of the lingua). Also present on its lateral margins were many papillae, all of which pointed backwards. The lingua consisted of 2 clearly defined parts, the corpus and the radix lingua, the portions being separated by a transverse row of papillae, the papillae linguales. Lying immediately behind the papillae linguales and the corpus lingua, was the mons laryngealis. Present on the rostral surface of the mons laryngealis was the glottis, situated directly ventral to the wide part of the choana. Situated behind the glottis were several rows of long backward-pointing papillae pharyngeales. The cavum oralis of all male Kori Bustards contained a saccus oralis which lay immediately beneath the skin of the neck. The large V-shaped opening to the saccus oralis was ventral to the radix lingua between the rami of the mandible. In 1 male bustard in breeding condition, the opening was 45 mm long and 32 mm at its widest point, and the diameter of the balloon-shaped pouch was 100 mm. Its colour was light pink with faint pigmentation and it was indented with small pinpoint nodules. The saccus oralis was absent in the males of other species of bustards examined in this study.

The oesophagus

The oesophagus was a long, muscular, longitudinally folded tube and usually lay to the right of the midline of the neck. It was mobile and had a markedly expansible diameter. Its structure was relatively uniform throughout. No crop was present in any of the species examined. The oesophagus connected the pharynx to the gastric region, and consisted of a proximal pars cervicalis and a distal pars thoracica. The pars thoracica opened into the proventriculus within the thoracoabdominal cavity. The length of the oesophagus of the male Houbara Bustard was significantly greater than that of the female ($P < 0.05$).

The stomach

The bustard stomach consisted of a cranial glandular compartment or proventriculus and a caudal muscular compartment or ventriculus (Figs 4–6, 14). The gross appearance of the proventriculus and ventriculus was similar in all species examined.

The proventriculus

The proventriculus was cone-shaped and arose from the oesophagus without a distinct demarcation. Faint hexagonal lines were often visible on the surface (Fig. 5). The wall was thicker than that of the oesophagus. The caudal extent of the proventriculus was marked by a constriction, the isthmus gastris. Examination of the mucosal surface of the proventriculus revealed the presence of raised papillae, papillae proventriculus, over its entire surface (Fig. 6). The mean length of the proventriculus of the male Houbara Bustard was slightly greater than that of the female, but the difference was not significant ($P > 0.05$).

The ventriculus

The ventriculus lay in the left dorsal and ventral regions of the thoracoabdominal cavity. When observed ventrally, the liver and the fat laden posthepatic septum obscured the abdominal organs (Figs 1–3). The ventriculus was oval-shaped and consisted of a body with 2 tapering ends, the saccus cranialis and saccus caudalis. The thick muscular walls consisted of the crassus caudodorsalis and crassus cranioventralis muscles (Figs 5, 14). A much thinner muscle layer, consisting of the tenuis craniodorsalis and caudoventralis muscles were present in the saccus cranialis and the saccus caudalis respectively. The pyloric region of the stomach, connecting the ventriculus and duodenum arose from the right face of the ventriculus. The inner aspect of the ventriculus was lined by a hardened membrane, the cuticula gastrica, which frequently appeared green due to the regurgitation of bile (Fig. 6). Small stones and grit were found in all species examined. The mean mass of the empty ventriculus of the male Houbara Bustard was significantly greater than that of the female ($P < 0.05$).

The small intestine

The small intestine comprised the duodenum, jejunum and ileum (Fig. 11). The duodenum formed a characteristic 'U'-shaped loop, the ansa duodenalis, consisting of descending and ascending limbs. The 2 loops of the duodenum were held together by a narrow fold of mesentery (Fig. 9). There was no distinct transition between the ascending duodenal limb and the jejunum. The jejunum was of the same width as the duodenum. The transition between the jejunum and ileum could not be determined. Diverticuli vitellini were not observed in the species examined. The ileum terminated at the ileocaecal opening. The dorsal mesentery supported the vasculature of the intestinal tract as well as the bile ducts and the spleen. When opened and washed free of intestinal mucus and debris, the internal surface of the small intestine presented a velvety appearance because of the villi that covered the entire surface. In both the Houbara Bustard and the Kori Bustard, the mean length of the small intestine was significantly greater in males compared with females ($P < 0.05$).

The caeca

The right and left caeca arose from the lateral walls of the rectum, close to the junction with the ileum (Fig. 11). They were well developed and were usually grey-green in colour. Each caecum could be divided externally into a short proximal neck, the cervix ceci, a long thin-walled body, the corpus ceci, and a short apex, the basis ceci. In both the Houbara Bustard and the Kori Bustard, the mean length of the caeca was again significantly greater in males compared with females ($P < 0.05$).

The rectum and cloaca

The rectum of all species of bustards was a short tube-like structure extending from the caudal end of the ileum, the point at which the paired caeca commenced. Whilst it was possible to distinguish the rectum from the ileum by its larger diameter, it continued indistinctly into the cloaca (Fig. 11). The vent appeared as a transverse slit opening from the cloaca. In both the Houbara Bustard and the Kori Bustard, the mean length of the combined rectum and cloaca was longer in males compared with females; the difference was not significant in Houbara Bustards ($P > 0.05$), but it was significant in Kori Bustards ($P < 0.05$).

The pancreas

The pancreas was a pale-yellow organ with a finely lobulated surface situated between 2 limbs of the duodenum and it was frequently hidden by fat. It consisted of 2 lobes lying dorsally (lobus pancreatis dorsalis), and ventrally (lobus pancreatis ventralis) (Figs 7, 8, 9). Well developed interlobar connections made it difficult to distinguish between the 2 lobes in most of the birds examined. However, in 2 Kori Bustards, the dorsal and ventral lobes were connected by a thin bridge of tissue and the lobes were clearly separated. In both Houbara Bustards and Kori Bustards the dorsal and ventral lobes were drained by a separate duct which opened into the distal part of the duodenum.

The liver

The liver consisted of left (lobus hepaticus sinister) and right (lobus hepaticus dexter) lobes which were joined cranially at the midline by an interlobar portion (pars interlobaris) (Fig. 10). The liver was characteristically dark red-brown in colour. The right lobe was larger than the left lobe, and there were no further lobular subdivisions. Stretching across the visceral surfaces of both lobes was a transverse groove from where the bile ducts emerged.

The anatomy of the bile ducts was recorded for the Houbara and Kori Bustard. One bile duct, the ductus hepatocysticus, originated from the right lobe of the liver and opened into an elongated, pear shaped gallbladder which drained via a single ductus cystico-entericus into the duodenum, distal to the pancreatic ducts (Figs 7, 8). The second bile duct, the ductus hepatoentericus emerged from the left lobe of the liver and drained into the duodenum between the pancreatic ducts (Figs 7, 8). In both the Houbara Bustard and the Kori Bustard, the mean liver mass was significantly greater in males compared with females ($P < 0.05$).

DISCUSSION

The structural characteristics of the avian gut are largely determined by the dietary preference of the species (Leopold, 1953; Moss, 1972). The bustards described in this report are opportunistic omnivores. In the wild they feed on a wide variety of terrestrial invertebrates and vegetable matter as well as small vertebrates such as lizards, rodents and snakes (Johnsgard, 1991). The captive birds used in this study were kept in naturalistic aviaries where it is known that approximately 25% of their diet consists of natural food from their surroundings, such as annual plants and terrestrial invertebrates (Warren, 1996). The well differentiated stomachs and well developed caeca of the bustard species examined in this study are characteristic of omnivores, although it is known that caecal length can show variation unrelated to food habits (Ziswiler & Farner, 1972; McLelland, 1979*a*).

Boulton (1864) commented on the presence of papillae on the lingua and the glottis of a great bustard and considered that they 'served principally as mechanical obstacles to the involuntary return of food that has passed over them'. In the current study well developed caudally directed papillae were present on the lingua, on the roof of the palate, and the mons laryngealis in all bustard species examined. In other species these papillae assist with swallowing and have evolved to move the bolus of food caudally and prevent regurgitation (McLelland, 1979*a*).

The morphology of the alimentary tract and the proportional contribution of each region were similar in all species of bustards examined. The oesophagus and the combined proventriculus and ventriculus form a greater proportion of the bustard alimentary tract compared with other avian species for which data are available. Bustards have long necks and possess no crop, which may explain the longer oesophagus, while the longer proventriculus and ventriculus may reflect an adaptation in the storage of food compared with other species. In ratites, the crop is also absent and the large proventriculus and ventriculus of these birds is considered to help with food storage (Angel et al. 1996). The small intestine of the bustard forms a smaller proportion of the total length of the alimentary tract compared with other avian species on a bodyweight basis (see Table 2; Leopold, 1953). These non-bustard species are herbivores or granivores, and it is known that omnivores tend to have a shorter, less complex digestive tract (Ziswiler & Farner, 1972). However, the small intestine of the Rufous-crested Bustard formed 55.1% of the alimentary tract, which is longer compared with the other bustards. The larger ventriculi and longer small intestine may be indicative of dietary differences.

The saccus oralis in the Kori Bustard has been previously described by Murie (1868, 1869) and in the Great Bustard by Flower (1865), Cullen (1865), and Beddard (1898). These are not reported to be concerned with carrying or storing food in any species of bustard and, instead, are used as display chambers during the breeding season (Murie, 1869). In the present study, food debris was not found in the saccus oralis of any of the male Kori Bustards. The authors have observed inflation of the upper cervical region in these birds during the breeding season. Sacci orali were not observed in the males of the other bustard species examined in this study.

The simplest form of crop is a spindle-shaped enlargement of the cranial, middle or caudal region of the oesophagus. McLelland (1979*a*) reported that some bustards belonging to the genus Otis had such an enlargement, but the species were not specified. Neither a crop nor an oesophageal enlargement was observed in the present study. Although food may be stored throughout the length of the oesophagus of avian species which have no crop (Ziswiler & Farner, 1972; McLelland, 1979*a*), no food remains were observed in the oesophageal lumen of the 38 bustards examined.

Ventriculus weights, including the cuticle, of Houbara and Kori Bustards ranged from 1.1 to 1.36% of bodyweight, which are lower compared with the Bantam Chickens where the ventriculus comprised 1.99% of bodyweight. They are also lower compared with the ventriculus weights (excluding the cuticle) of the Domestic Turkey and Fowl which comprise from 1.91 to 2.4 % and from 1.49 to 2.18 % of bodyweight respectively (Latimer & Rosenbaum, 1926; Hafez, 1955). The ventriculus weight of Rufous-crested Bustards was 2.21 % bodyweight, approximately twice as large as that of the Kori and Houbara Bustards, and similar to that of the Domestic Fowl and Turkey. The weight of the ventriculus is an expression of the development of its muscular wall, which in turn is related to the type of food consumed (McLelland, 1979*a*). All bustards examined had stones of various sizes present in the ventriculi, probably ingested deliberately to assist with the grinding down of food. Free-ranging Houbara Bustard have been observed picking up small reddish particles on the surface of desert sand (Surahio, 1985).

The rectum and cloaca formed a greater proportion of the bustard alimentary tract compared with the Bantam Chicken. The large intestine plays a major role in resorption of water and these data may reflect an adaptation for water conservation in bustards. Earlier examinations of the bustard alimentary tract have described the hindgut and caeca as being extremely capacious (Mitchell, 1901), and short (Mitchell, 1895). Beddard (1910) later demonstrated that the alimentary tracts of various bustard species were uniform. Whilst our studies generally support the findings of Mitchell (1901) and Beddard (1910), observations of the morphology of the caeca appear to differ. Previous descriptions of the caeca of the great bustard have classified it as either sacculated (Maumus, 1902), or long and sacculated (McLelland, 1989). Although the caeca were well developed in all 4 species of bustards examined in this study, no sacculations were observed.

Bustards display sexual dimorphism and males are generally larger than females. McLelland (1979*a*) reported that intestinal length varied with sex in some species of birds. All alimentary tract parameters described in this study showed sexual dimorphism where male and female data were available for direct comparison. Previous studies on bustards did not specify the sex of the birds examined (Beddard, 1898; Maloiy et al. 1987) and based on our findings we recommend that the bustard alimentary tract should be analysed separately according to sex.

Boulton (1864) considered that the liver of the Great Bustard appeared to be large in proportion to the size of the bird, while Beddard (1898) noted that the right lobe of the liver of Tetrax was larger than the left lobe. In the species examined in the current study the right lobe of the liver was found to be the larger lobe, and unlike the domestic fowl, no lobe was subdivided into a dorsal and ventral part (King & McLelland, 1984). The proportion of bustard liver weight to total bodyweight (1.41–2.1 % of total bodyweight) is similar to that of domestic fowl and turkey in which the liver forms 1.7–3.7 % of total bodyweight (Latimer & Rosenbaum, 1926; Hafez, 1955; Al Dabagh & Abdulla, 1963; McLelland, 1979*a*). The size, weight, consistency and colour of the liver are dependent on the breed, age and nutritional status of the individual bird (Nickel et al. 1977). The type of food consumed appears to have an important correlation with liver size, with insectivores and piscivores having the largest livers relative to body size (McLelland, 1979*a*). A previous study reported that Kori Bustards had a single bile duct formed by the ductus cysticoentericus and ductus hepatoentericus which opened into the duodenum (Maloiy et al. 1987). In the current study, the ductus cysticoentericus and ductus hepatoentericus drained separately into the duodenum of Kori Bustards.

Pancreas size of bustards (0.074–0.094 % of bodyweight) appears to be considerably lower compared with chicken and turkey (*Meleagris gallopavo*) in which the pancreas forms about 0.12–0.29 % of total bodyweight (Latimer & Rosenbaum, 1926; Hafez, 1955; McLelland, 1979*a*). The significance of this finding in bustards is unknown although pancreas size is reported to be smaller in carnivores and granivores (McLelland, 1979*a*). Whilst the Kori Bustard pancreas in previous studies was reported to drain by a single duct (Maloiy et al. 1987), the pancreas in our study was found to drain by 2 ducts arising separately from the dorsal and ventral lobes and opening separately into the duodenum.

The aim of captive breeding and restoration programmes like NARC is to breed and release surplus bustards to supplement declining free-living populations. It is known that small intestinal and cecal lengths of red grouse (*Lagopus lagopus scoticus*), derived from the wild, decrease over successive generations when maintained in captivity because of the change in diet (Moss, 1972). Changes in gastrointestinal morphology induced as a consequence of captivity could be a factor influencing the survival of released captive-reared birds. However, data on the morphology of the alimentary tract of captive and free-living bustards are scarce. The only published data of alimentary tract lengths of free-living bustards was the study performed on 3 Kori Bustards by Maloiy et al. (1987). These birds were captured in the wild, but were held in captivity on a meat diet for 2 wk before euthanasia. Although neither the sex and age of the birds was specified, their mean bodyweight was 8 kg (Maloiy et al. 1987), which is similar to the combined mean bodyweight of male and female Kori Bustards (7.3 kg) described in this study. Compared with the combined male and female intestine length data from captive birds described in this study, free-living kori had longer small intestines (1137 mm against 971 mm) but shorter large intestines (199 mm against 210 mm) and ceca (240 mm against 280 mm). Further data on alimentary tract measurements of free-living bustards is required to establish if differences exist between free-living and captive birds and to assess if these differences could influence the survival of released birds.

The main findings of this study can be summarised as follows. (1) The morphology of the alimentary tract was similar in all species examined, although male Kori Bustards possessed a saccus oralis in the oropharyngeal cavity that was not present in the other species. (2) The proportions of the components of the alimentary tract were similar in all species examined. However, the data from the Rufous-crested Bustards showed minor differences compared with the other bustards (comparatively larger ventriculi and longer small intestines) that may indicate dietary differences between the species. (3) Length and weight measurements of each component of the alimentary tract showed sexual dimorphism in species where there was sufficient data for direct comparison. (4) Papillae in the cavum oralis and pharynx were well developed in all species examined. (5) No crop or oesophageal enlargement were observed in any of the species examined. (6) The oesophagus, proventriculus, ventriculus, ceca and large intestine were well developed in all species examined. (7) The small intestine was shorter than those of other herbivores and granivores when compared on a bodyweight basis. (8) No sacculations were observed on the caeca of any species examined.

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